

## Research



**Cite this article:** Schweinfurth MK, Taborsky M. 2018 Relatedness decreases and reciprocity increases cooperation in Norway rats. *Proc. R. Soc. B* **285**: 20180035. <http://dx.doi.org/10.1098/rsob.2018.0035>

Received: 5 January 2018

Accepted: 9 February 2018

**Subject Category:**

Behaviour

**Subject Areas:**

behaviour, cognition, evolution

**Keywords:**

reciprocity, kin selection, Norway rats, cooperation, iterated Prisoner's dilemma

**Author for correspondence:**

Manon K. Schweinfurth

e-mail: [manon.schweinfurth@iee.unibe.ch](mailto:manon.schweinfurth@iee.unibe.ch)

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4007635>.

# Relatedness decreases and reciprocity increases cooperation in Norway rats

Manon K. Schweinfurth<sup>1,2</sup> and Michael Taborsky<sup>1</sup>

<sup>1</sup>Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland

<sup>2</sup>School of Psychology & Neuroscience, University of St Andrews, Westburn Lane, KY16 9JP St Andrews, UK

MKS, 0000-0003-2066-7892; MT, 0000-0002-1357-4316

Kin selection and reciprocity are two mechanisms underlying the evolution of cooperation, but the relative importance of kinship and reciprocity for decisions to cooperate are yet unclear for most cases of cooperation. Here, we experimentally tested the relative importance of relatedness and received cooperation for decisions to help a conspecific in wild-type Norway rats (*Rattus norvegicus*). Test rats provided more food to non-kin than to siblings, and they generally donated more food to previously helpful social partners than to those that had refused help. The rats thus applied reciprocal cooperation rules irrespective of relatedness, highlighting the importance of reciprocal help for cooperative interactions among both related and unrelated conspecifics.

## 1. Introduction

Evolutionary theory predicts prevalence of selfish traits geared to outcompete rivals [1]. Hence, it is difficult to explain the evolution of traits that benefit others at the expense of their bearer. Nevertheless, apparently altruistic behaviours, entailing immediate costs without compensation by immediate benefits, are widespread in nature [2]. Indirect fitness gains through promoting relatives are commonly assumed to play the major role in the evolution of such behaviours (e.g. [3]). However, help occurring between unrelated individuals usually cannot be explained by indirect fitness effects and hence their evolution by kin selection. Hitherto, the empirical study of evolutionary mechanisms underlying cooperative and altruistic behaviours has happened more or less separately and in parallel between contexts, involving either related or unrelated individuals (e.g. [4,5]). Therefore, the relative importance of, and the possible interactions between these two mechanisms need experimental scrutiny.

Animals living in stable groups often interact with social partners varying in relatedness. Studies investigating reciprocal exchanges among group members have typically attempted to control for kinship to avoid ambiguous explanations [4]. We should not be misled to believe, however, that kin selection and reciprocity are mutually exclusive evolutionary mechanisms [6,7]. Indeed, it is likely that direct fitness benefits play an important role also in groups of relatives (reviewed in [5]). Empirical studies comparing the importance of reciprocity and relatedness for cooperation in primates, bats and cichlid fish revealed that cooperation among members of groups varying in relatedness can be better explained by reciprocity than by kin biases [8–10]. In addition, a comparative study of primates including humans has suggested that food-sharing is explained by kinship and reciprocity to comparable degrees [11]. Depending on the approach and respective assumptions, theoretical models predict either a similar or unequal contribution of reciprocity and kin nepotism to the evolution of cooperation [12–16], and there may be interactive effects between these mechanisms [17]. Despite the obvious interest in this subject in evolutionary biology, there is a lack of empirical studies attempting to disentangle effects of kinship from those of prior helping experience under

completely controlled experimental conditions (i.e. where both relatedness and behavioural outcomes are manipulated by the experimenter).

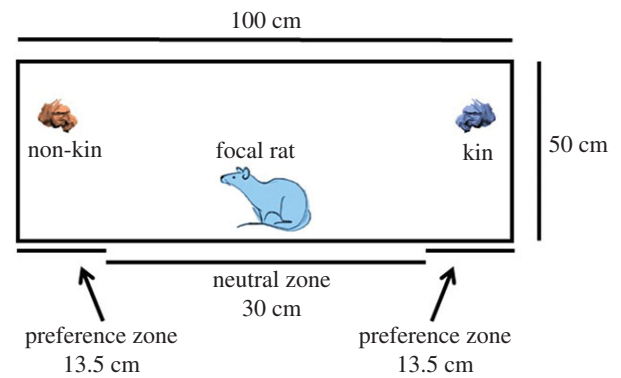
To fill this gap, we used male wild-type Norway rats (*Rattus norvegicus*) to experimentally study the relative importance of kin nepotism and reciprocity underlying food donations. Rats are highly social animals living in groups that consist of related and unrelated individuals [18]. Furthermore, they donate food to unrelated and unfamiliar conspecifics in variants of the iterated Prisoners' dilemma paradigm (IPD) and they allogroom social partners according to direct reciprocity rules [19–24]. Reciprocal interactions were shown to raise longevity of rats, highlighting potential fitness effects of reciprocity [25]. In the current experiment, rats were enabled to donate food to unfamiliar kin and unfamiliar non-kin that had been cooperative in one and defecting in another previous trial. If kin nepotism and reciprocity were mutually exclusive mechanisms, reciprocal trading should occur only among non-kin, whereas related individuals should cooperate independently of previously experienced cooperation. Alternatively, if these mechanisms work independently there should be no difference between reciprocal food exchange among related and unrelated individuals. Finally, if both mechanisms interact, kinship could either increase or decrease the decisions to reciprocate received favours.

Under semi-natural conditions, rats associate with related and unrelated individuals [18]. To ensure that experimental rats can discriminate kin from non-kin we conducted first an odour preference test. In the second experiment, we tested for the relative importance of relatedness and previously received help on food provisioning of a social partner. During the experience phase, focal rats experienced two different unfamiliar social partners that were either cooperating or defecting. These partners were either unrelated or related (full brothers) to the focal rat. Both related and unrelated partners provided food to the focal rat by pulling a platform equipped with an oat flake into the reach of the focal rat, i.e. they cooperated, or the platform was blocked, i.e. they defected. Immediately thereafter, focal rats were enabled to provide food to the previously experienced partners.

## 2. Material and methods

### (a) Experimental subjects and holding conditions

We used 19-month-old outbred wild-type male Norway rats (source: Animal Physiology Department, University of Groningen, Netherlands) with an average weight of 607 g. The rats were habituated to handling from weaning onwards and hence did not show any signs of stress when being handled, transported, exposed to the set-up or an observer. They were individually marked by ear punches. Brothers had been separated right after weaning with an age of five weeks and were afterwards housed in groups of four unrelated littermates. After the separation, rats never had any direct interaction with relatives. Housing cages measured  $80 \times 50 \times 37.5$  cm and were separated from each other through opaque walls to limit interactions between the groups. The ambient temperature was  $20^\circ\text{C} \pm 1^\circ\text{C}$ , with a relative humidity of 50–60%. The 12:12 h light/dark cycle was reversed, with lights on at 20.00 hours and 30 min of dusk and dawn. All training and experiments were conducted under red light during the dark phase of the daily cycle because rats are nocturnal [26] and lack red light receptors [27].



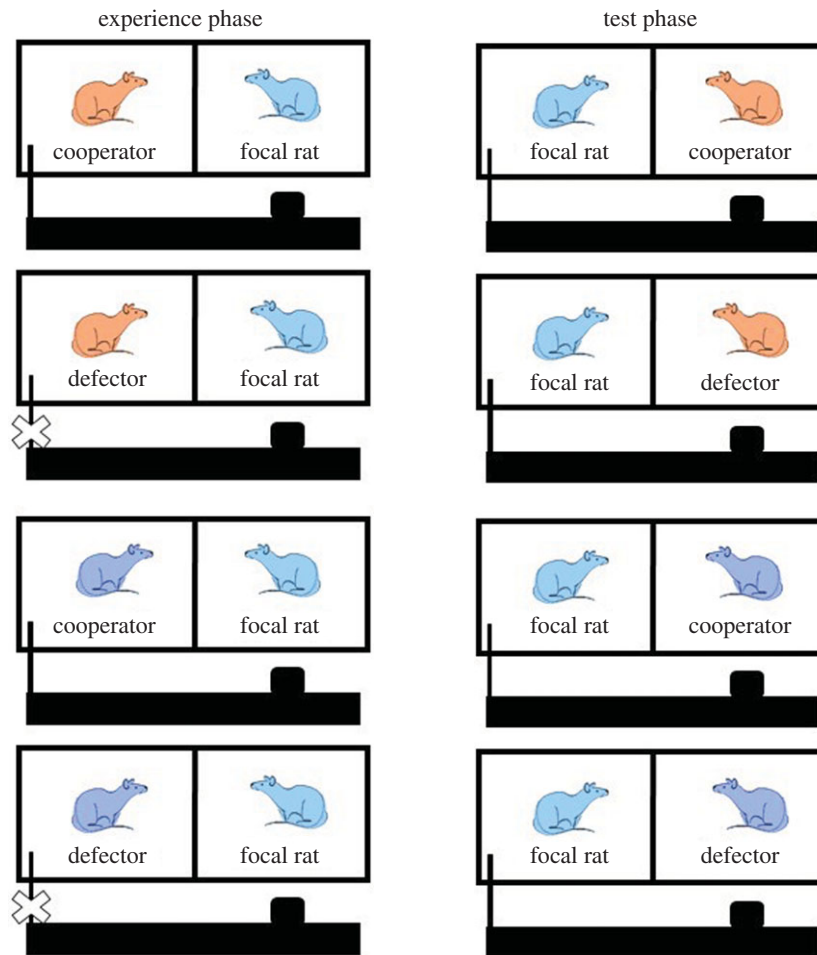
**Figure 1.** Set-up of kin discrimination test in experimental subjects. The experimental arena was supplied with one paper towel each on both sides (preference zone;  $13.5 \times 50$  cm). On these sides, we presented olfactory stimuli from two individuals simultaneously that were either brothers from, or unrelated to, the focal rats. Focal rats were released in the middle of the arena (neutral zone;  $60 \times 50$  cm) and time spent and autogrooming shown in each zone were measured for 10 min.

### (b) Kin discrimination test

To ensure that experimental rats were able to discriminate kin from non-kin we conducted a pre-test in a glass arena ( $100 \times 50 \times 50$  cm; figure 1). On the arena walls, we marked three zones using black permanent markers: a neutral zone ( $60 \times 50$  cm) in the middle and two preference zones ( $13.5 \times 50$  cm each) on the left and right sides of the arena. We collected olfactory stimuli from two individuals simultaneously that were a brother of, or unrelated to, the test rats. Odour was collected by petting these individuals with a paper towel (recycling-tissue: Oeco Swiss plus -3 layers) for 1 min each. Experimenters wore rubber gloves (Kimtech powder-free latex gloves) in order to avoid olfactory contamination of the towels. Then we placed one paper towel each in the two preference zones that contained either kin or non-kin odour. Thereafter, the focal rat was released into the neutral zone. We recorded its behaviour for 10 min using a Sony-handycam (HDR-CX550) with night vision mode. Videos were analysed with Solomon Coder version beta 15.11.19. The sides of the stimulus cues were chosen randomly, however, we ensured that kin odours were presented in both preference zones equally often. The observer was blind to the sides of the presented odour stimuli in the video recordings. After each trial, the glass arena was cleaned with 70% ethanol. In total, we used 32 focal rats. Donors of non-kin cues were taken from the same housing groups as donors of kin cues in order to avoid cage effects. We recorded how much time focal rats spent in each zone and the duration of autogrooming shown when present in these zones; autogrooming is reduced when animals are stressed and hence it may indicate relaxation [28]. We defined a rat being in the preference zone when all four paws were in a zone. We had to exclude seven focal rats from the analysis because they repeatedly destroyed the paper towels and removed them from the preference zones (hence  $n_{\text{total}} = 25$ ).

### (c) Pre-experimental training for food sharing

The experimental set-up followed Rutte & Taborsky [20] and was based on a two-player sequential food-exchange task [29]. Test cages ( $80 \times 50 \times 37.5$  cm) were divided into two compartments by a wire mesh. Rats were trained individually, and the training was divided into two parts: first, every single rat was trained to produce a reward (one oat flake) for itself. To get the reward, the rat learned to pull a stick fixed on a movable platform, which thereby slid into the cage. In the second training phase, rats were paired with a training partner on the other side of the



**Figure 2.** Experimental set-up to investigate the influence of reciprocity and relatedness on food donations. Rats could provide food to each other by pulling a stick that was connected to a movable platform that provided food only to the partner (recipient). During the experience phase, each focal rat experienced two partners in two situations. One partner was unrelated (indicated in red) and provided food (cooperator) to the focal rat or, when the platform was blocked (indicated by a cross), did not provide food (defector). During the test phase, the roles were exchanged, and the focal rat could provide food to the previously experienced respective partner. We followed the same procedure with a related partner (indicated in blue). All focal rats experienced all four situations in a random sequence.

wire mesh and learned over 18 sessions to provide food for this partner, and vice versa. Roles were exchanged and the intervals between these switches were increased gradually from one single pull to a pulling period of 7 min. For a detailed description of this training see [30]. The donor did not receive a reward for its pulling effort, but only its partner, which could subsequently return received provisions. In contrast to the experiment, in which kin and non-kin partners were unfamiliar to each other, training partners originated from the same housing group and were thus familiar to each other.

#### (d) Influence of relatedness and reciprocity on food provisioning

This experiment consisted of an experience and a test phase (figure 2). During the experience phase, focal rats ( $n = 21$ ; 26 individuals were originally tested, however 5 had to be excluded as these rats never pulled in any of the trials) experienced two different unfamiliar social partners that were either cooperating or defecting. These partners were either unrelated or related (full brothers) to the focal rats. Both related and unrelated partners provided food to the focal rat during 7 min of the experience phase by pulling the platform equipped with an oat flake into the reach of focal rats, i.e. they cooperated. The number of food donations was decided by the partner rat and was not fixed by the experimenter. In a second trial, the same partner was hindered to provide food to focal rats by blocking

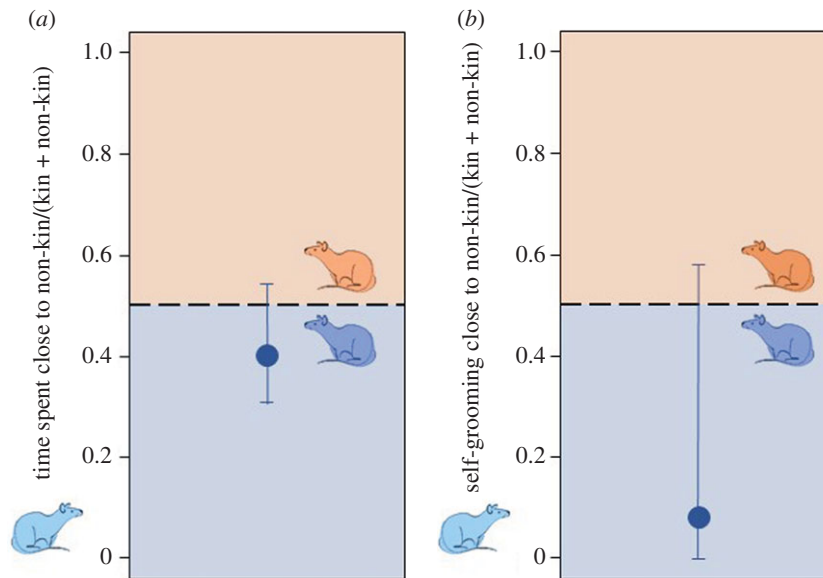
the platform, i.e. they defected. Therefore, focal rats experienced in a random sequence: a cooperating kin, cooperating non-kin, defecting kin, and defecting non-kin social partner. Immediately thereafter, focal rats were enabled to provide food to the previously experienced partners for 7 min and we counted how often they provided food to their partners during this test period.

The test order of focal individuals and of treatments was selected randomly using Excel. However, we made certain that each treatment was tested equally often on each day and we kept the random order of individuals over all treatments. The experimenter was blind to the relatedness between focal and partner rats.

#### (e) Statistical analyses

All statistical analyses were performed with R (v. 2.15.2, <http://www.r-project.org/>; with R studio, packages: 'lme4'). All test results report two-tailed  $p$ -values.

To test whether rats distinguish kin from non-kin in the pre-test, we calculated an index for overall time spent in each preference zone and for time spent autogrooming. For this, we divided the times in the preference zone with non-kin odour by the time spent in both preference zones combined. The distribution of time indices did not significantly deviate from a normal distribution (Shapiro–Wilk test:  $W = 0.95$ ,  $p = 0.30$ ). We therefore conducted a parametric one-sample  $t$ -test against the null hypothesis of an equal distribution of 0.5. Because the data for the autogrooming index differed from a normal distribution



**Figure 3.** Kin discrimination. Rats spent more time (a) and groomed themselves longer (b) close to kin odour than in the zone containing non-kin odour. The dashed line marks a random choice at 0.5 and the blue zone indicates time close to kin whereas the red zone depicts time next to unrelated individuals. Median durations are shown with interquartile ranges.

(Shapiro–Wilk test:  $W = 0.69$ ,  $p < 0.001$ ), we followed the same procedure using a non-parametric one-sample Wilcoxon test.

To test whether reciprocal cooperation was influenced by relatedness between partners, we conducted a generalized linear mixed model (GLMM). We included the focal rats' frequency to provide food as a dependent variable and assumed a Poisson distribution, as the zero-inflated count data were not normally distributed (Shapiro–Wilk normality test:  $W = 0.89$ ,  $p < 0.0001$ ). Relatedness (kin or non-kin) and cooperation level of partners (cooperating or defecting) were used as fixed factors. The identity of the respective focal rat was included as a random effect to correct for testing the same individual in four different treatments. We further included a random effect, which was pair number nested in focal rat, because we used eight rats as both focal and partner rats and thereby controlled for the multiple usage. The behaviour of no rat appears more than once in the dependent variable, so pseudoreplication was avoided. We removed the non-significant interaction term between relatedness and cooperation level (GLMM:  $\beta = -0.02 \pm 0.26$ ,  $X^2 = 0.01$ ,  $p = 0.90$ ) and report the reduced model [31].

Further, we tested whether related and unrelated partners differed in other aspects such as proximity and shared investigation time, which might affect helping levels. We checked for potential differences in (i) proximity, defined by a minimum distance to the dividing mesh of 5 cm of the partner's body excluding the tail, and (ii) shared investigation time, defined by the focal individual and its partner sniffing simultaneously at each other through the mesh. The behaviours were coded from video recordings, which were available from only half the dataset. We compared the related and unrelated partners with linear mixed models. To approximate normality in the model residuals, the investigation time was log transformed, which was not required for the time in proximity. We included relatedness (kin or non-kin) as a fixed factor and two random effects as described above.

### 3. Results

#### (a) Kin discrimination test

Focal rats spent more time in a preference zone close to the odour of a brother than in a corresponding zone close to the odour of an unrelated individual (One sample *t*-test,

two-tailed:  $n = 25$ ,  $t = -2.24$ ,  $p = 0.035$ , figure 3a). Furthermore, they spent more time autogrooming when close to kin odour than when close to non-kin odour (One sample Wilcoxon-test, two-tailed:  $n = 25$ ,  $V = 84$ ,  $p = 0.031$ , figure 3b).

#### (b) Influence of relatedness and reciprocity on food provisioning

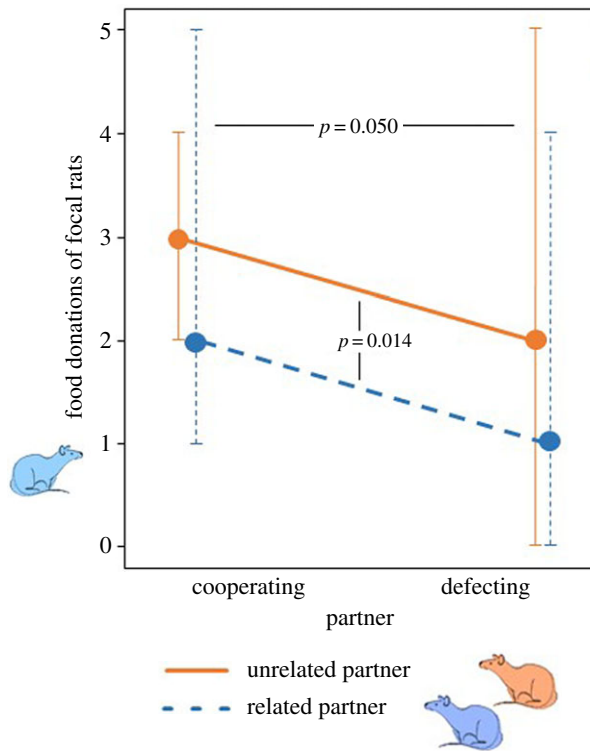
The focal rats helped unrelated partners more often than related individuals (GLMM:  $\beta = 0.32 \pm 0.13$ ,  $X^2 = 6.00$ ,  $n = 21$ ,  $p = 0.014$ , figure 4 and electronic supplementary material, figure S1). Focal rats provided less food to previously defecting partners than to cooperating ones, thereby using decision rules of direct reciprocity (GLMM:  $\beta = -0.25 \pm 0.13$ ,  $X^2 = 3.73$ ,  $n = 21$ ,  $p = 0.050$ , figure 4 and electronic supplementary material, figure S1). This causal link was not influenced by relatedness, as indicated by the non-significant interaction term (GLMM:  $\beta = -0.02 \pm 0.26$ ,  $X^2 = 0.01$ ,  $p = 0.90$ ).

Neither the time in proximity (LMM:  $\beta = -3.25 \pm 15.85$ ,  $X^2 = 0.04$ ,  $p = 0.83$ , electronic supplementary material, figure S2) nor the investigation time (LMM:  $\beta = -4.85 \pm 4.55$ ,  $X^2 = 1.15$ ,  $p = 0.28$ , electronic supplementary material, figure S2) differed between related and unrelated partners.

### 4. Discussion

Our aim was to clarify the interplay between effects of previous experience and relatedness on decisions to provide help to a social partner. Therefore, we tested first whether rats discriminate kin from non-kin. We found that adult male rats recognize relatives by body odour even after 15 months of separation, which confirms the olfactory recognition competence of rats as shown in other contexts (e.g. [32]). Next, we tested whether helping rates of focal subjects differ between related and unrelated partners when these had been cooperative before or not. Rats donated more food to previously helpful food providers compared to previously





**Figure 4.** Reciprocal food donations to related and unrelated social partners. Rats donated more food to previously cooperating than to previously defecting partners (abscissa), irrespective of relatedness. Rats donated overall more food to unrelated rats (solid line) than to related social partners (dashed line). The graph shows the median numbers of donations ( $\pm$  interquartile ranges) of focal rats during the test phase.

non-helpful individuals, which reveals that they applied direct reciprocity rules. This is consistent with previous studies using solely unrelated rats [20–23,30,33]. However, although the focal subjects reciprocated food donations with both types of cooperative partners, they provided more food to unrelated partners than to their brothers.

The higher propensity to help unrelated than related partners cannot be explained by a greater distraction by relatives, because proximity and investigation times were similar towards related and unrelated partners. Instead, this result might reflect an adaptive response based on either coercion, commodity trading, or correlated pay-offs. Firstly, if help is aggressively enforced by a prospective receiver, relatedness should mitigate coercion because of the aligned fitness interests of close kin [15]. Indeed, relatedness and coercion correlate negatively with each other in eusocial insects [34]. In banded mongooses (*Mungos mungo*), subordinate females that are closely related to the dominants are attacked more severely and evicted more often from the group compared to unrelated females that invest more in resisting such attacks [35]. In cooperatively breeding cichlids, where alloparental care of subordinates is traded against resource access and anti-predator protection by dominant group members who control the cooperative behaviour of subordinates through punishment of idle helpers, relatedness alleviates cooperation [10,36,37]. Female Norway rats were also shown to increase their helping propensity in response to aggression received from previous defectors in a similar experimental paradigm as used in this study [30]. However, in our experiment no obvious aggression was shown, hence there was no indication that rats coerced help from their partners.

Secondly, rats may trade social tolerance against food donations (e.g. [38]). Under semi-natural conditions, rats may cluster with kin [39], although not exclusively so [40]. By providing overall more help to unrelated than to related individuals, rats might appease them, which may not be needed as much in relatives (for a similar argument see [10,15]). Finally, repeated interactions between the same individuals may cause cooperation by correlated pay-offs [5]. Because relatives share fitness interests through genetic similarity [41], providing benefits to a related partner is not a prerequisite for expecting the partner to be cooperative in a future interaction. In contrast, being helpful to an unrelated partner can be a useful means to increase the chances of receiving help in return when this will be needed in the future [7]. Therefore, reciprocity may play a more important role between unrelated than among related individuals (see [42] for a theoretical treatment). In other words, benefits are correlated between repeatedly interacting social partners *either* by relatedness *or* by providing and reciprocating service [5,15].

These three lines of arguments can explain why helping levels are sometimes reduced between kin. However, all three concepts would rather predict an interaction between relatedness and reciprocity with crossing reaction norms, which was not shown by our data. We can safely conclude from our results that relatedness decreases the propensity of rats to help a partner obtain food, whereas it does not influence their decisions to return received help. It will be a worthwhile challenge for future studies to unveil under which conditions reciprocity is selected among both kin and non-kin, while kinship diminishes overall helping levels independently of the decision to reciprocate received favours.

It has been argued that reduced helping levels towards related individuals might result also from increased competition between kin ([43], reviewed in [44]). Rats have been reported to form subgroups [39], and here relatives may compete more intensely over resources than members of different groups. Food distribution can be very patchy for rats, leading to high local competition (e.g. [45]). Under such conditions, high competition between kin may cancel out the otherwise enhancing effect of relatedness on cooperation [46]. However, this cannot explain why help is *reduced* towards kin as compared to non-kin. In addition, the models explaining reduced help due to local competition among kin have been challenged due to their specific assumptions [14]. Hence, it seems unlikely that adaptations to local kin competition can explain our results.

In general, kin selection may provide a less straightforward explanation of cooperative behaviour among group members than has been assumed. This is reflected also by empirical results [8–10,15]. For instance, humans reported in questionnaires to reciprocate help with both related and unrelated individuals, but they showed a higher motivation to provide low-cost help to unrelated social partners than to relatives [47]. This pattern was reversed, however, if the costs of help were increased [47]. This suggests that the costs of helping, which were low in our experiment as well, may affect the interplay of relatedness and previous experience on helping propensity [48]. Incidentally, Norway rats were shown also to take into account the costs of cooperation when reciprocating help to unrelated partners [21]. The intricate interplay between direct and indirect fitness benefits of helping behaviour can be illustrated also in cooperatively breeding species, where subordinates help raising the

offspring of dominants. Helpers typically vary in relatedness to the young they care for. While in some species helpers preferentially support kin (e.g. [49]), help towards unrelated offspring is also well documented [50]. Kin selection predicts that variation in relatedness to receivers should reflect the amount of provided help [3,51], but evidence for this is mixed. For instance, in cooperatively breeding fish, relatedness *reduces* the propensity of helpers to invest in alloparental care [10]. Taken together, direct fitness benefits can select for higher levels of cooperation among social partners than indirect benefits [36], as confirmed by theoretical models [15].

Importantly, our results also show that related individuals reciprocate food donations, which contrasts with the default assumption that cooperation between kin is always based on kin selection (cf., [8]). Just like other social partners, related group members may also compete for resources such as food, shelter or mates and therefore lower the benefits of kin-biased altruism. This may render relatedness rather unimportant in repeated interactions among social partners. For instance, chimpanzees were shown to disregard relatedness when exchanging prosocial tokens [52], and food donations among vampire bats were better explained by previous receipt of help than by relatedness [9]. Together with our study, these results suggest that direct fitness benefits may be often more important for cooperation decisions than indirect fitness benefits.

## 5. Conclusion

Food donations of our rats were influenced by their partners' relatedness and by received help, indicating that in rats both mechanisms concurrently affect food donations. However,

contrary to scientific consensus kinship did not enhance but reduce cooperation propensity, while both unrelated and related individuals exchanged help by applying direct reciprocity rules. This is reminiscent of human behaviour, if helping others implies low costs [47]. This resemblance might indicate conserved evolutionary pathways of cooperation across a wide range of taxa.

**Ethics.** In accordance with animal welfare legislation of Switzerland (Tierschutzverordnung Schweiz 04/2008) we kept the rats in enriched cages containing various materials (a wooden house and board, a plastic tube, a piece of wood to nibble, a paper roll to play, digging-material (wood shavings), nest-building material (hay) and a salt block) [53]. Food (conventional rat pellets, and corn mix alternating with fresh fruits and vegetables) was provided every evening after the tests. All rats were food deprived for 10 h prior to the food-donation experiment during their inactive phase after receiving corn, but always had access to water *ad libitum*. Rats were kept in small groups with a maximum of four individuals per cage [54]. Animal housing and experimentation were approved by and conducted in accordance with the guidelines set by the Swiss Federal Veterinary Office under licence BE25/14. In our experiments, there was no possibility of physical contact between the test individuals due to a wire mesh separating the experimental compartments, and no injuries occurred.

**Data accessibility.** The data reported in the paper can be found in the electronic supplementary material.

**Authors' contributions.** M.T. and M.K.S. designed the experiment and wrote the paper; M.K.S. collected and analysed the data.

**Competing interests.** The authors declare no competing interests.

**Funding.** Funding was provided by SNF-grant no. 31003A\_156152 to M.T.

**Acknowledgements.** We thank Pia Stettler and Claudia Blumenstein for collecting data on the first test, Evi Zwygart for help with animal care, Valentina Balzarini for drawings, Leif Engqvist for statistical advice, and Joachim Frommen and Frank Groenewoud for comments on the manuscript.

## References

- Darwin C. 1859 *On the origins of species*. London, UK: John Murray.
- Trivers RL. 1985 *Social evolution*. Michigan: Benjamin/Cummings Publishing.
- Bourke AFG. 2014 Hamilton's rule and the causes of social evolution. *Phil. Trans. R. Soc. B* **369**, 20130362. (doi:10.1098/rstb.2013.0362)
- Schino G, Aureli F. 2010 A few misunderstandings about reciprocal altruism. *Commun. Integr. Biol.* **3**, 561–563. (doi:10.4161/cib.3.6.12977)
- Taborsky M, Frommen JG, Riehl C. 2016 Correlated pay-offs are key to cooperation. *Phil. Trans. R. Soc. B* **371**, 20150084. (doi:10.1098/rstb.2015.0084)
- Carter GG, Wilkinson GS, Page RA. 2017 Food-sharing vampire bats are more nepotistic under conditions of perceived risk. *Behav. Ecol.* **28**, 565–569. (doi:10.1093/beheco/ax006)
- Carter GG, Farine DR, Wilkinson GS. 2017 Social bet-hedging in vampire bats. *Biol. Lett.* **13**, 20170112. (doi:10.1098/rsbl.2017.0112)
- Schino G, Aureli F. 2010 The relative roles of kinship and reciprocity in explaining primate altruism. *Ecol. Lett.* **13**, 45–50. (doi:10.1111/j.1461-0248.2009.01396.x)
- Carter GG, Wilkinson GS. 2013 Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc. R. Soc. B* **280**, 20122573. (doi:10.1098/rspb.2012.2573)
- Zöttl M, Heg D, Chervet N, Taborsky M. 2013 Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nat. Commun.* **4**, 1341. (doi:10.1038/ncomms2344)
- Jaeggi AV, Gurven M. 2013 Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proc. R. Soc. B* **280**, 20131615. (doi:10.1098/rspb.2013.1615)
- Fletcher JA, Zwick M. 2006 Unifying the theories of inclusive fitness and reciprocal altruism. *Am. Nat.* **168**, 252–262. (doi:10.1086/506529)
- van Veelen M, Garcia J, Rand DG, Nowak MA. 2012 Direct reciprocity in structured populations. *Proc. Natl Acad. Sci. USA* **109**, 9929–9934. (doi:10.1073/pnas.1206694109)
- Lehmann L, Rousset F. 2010 How life history and demography promote or inhibit the evolution of helping behaviours. *Phil. Trans. R. Soc. B* **365**, 2599–2617. (doi:10.1098/rstb.2010.0138)
- Quinones AE, van Doorn GS, Pen I, Weissing FJ, Taborsky M. 2016 Negotiation and appeasement can be more effective drivers of sociality than kin selection. *Phil. Trans. R. Soc. B* **371**, 20150089. (doi:10.1098/rstb.2015.0089)
- Queller DC. 1985 Kinship, reciprocity and synergism in the evolution of social behaviour. *Nature* **318**, 366–367. (doi:10.1038/318366a0)
- van Cleve J, Akçay E. 2014 Pathways to social evolution: reciprocity, relatedness, and synergy. *Evolution* **68**, 2245–2258. (doi:10.1111/evo.12438)
- Gardner-Santana LC, Norris DE, Fornadel CM, Hinson ER, Klein SL, Glass GE. 2009 Commensal ecology, urban landscapes, and their influence on the genetic characteristics of city-dwelling Norway rats (*Rattus norvegicus*). *Mol. Ecol.* **18**, 2766–2778. (doi:10.1111/j.1365-294X.2009.04232.x)
- Wood RI, Kim JY, Li GR. 2016 Cooperation in rats playing the iterated Prisoner's dilemma game. *Anim. Behav.* **114**, 27–35. (doi:10.1016/j.anbehav.2016.01.010)
- Rutte C, Taborsky M. 2008 The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity. *Behav.*

- Ecol. Sociobiol.* **62**, 499–505. (doi:10.1007/s00265-007-0474-3)
21. Schneeberger K, Dietz M, Taborsky M. 2012 Reciprocal cooperation between unrelated rats depends on cost to donor and benefit to recipient. *BMC Evol. Biol.* **12**, 41. (doi:10.1186/1471-2148-12-41)
  22. Schweinfurth MK, Taborsky M. 2017 The transfer of alternative tasks in reciprocal cooperation. *Anim. Behav.* **131**, 35–41. (doi:10.1016/j.anbehav.2017.07.007)
  23. Dolivo V, Taborsky M. 2015 Norway rats reciprocate help according to the quality of help they received. *Biol. Lett.* **11**, 20140959. (doi:10.1098/rsbl.2014.0959)
  24. Schweinfurth MK, Stieger B, Taborsky M. 2017 Experimental evidence for reciprocity in allogrooming among wild-type Norway rats. *Sci. Rep.* **7**, 4010. (doi:10.1038/s41598-017-03841-3)
  25. Yee JR, Cavigelli SA, Delgado B, McClintock MK. 2008 Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosom. Med.* **70**, 1050–1059. (doi:10.1097/PSY.0b013e31818425fb)
  26. Norton S, Culver B, Mullenix P. 1975 Development of nocturnal behavior in albino rats. *Behav. Biol.* **15**, 317–331. (doi:10.1016/S0091-6773(75)91717-4)
  27. Yokoyama S, Radlwimmer FB. 1998 The ‘five-sites’ rule and the evolution of red and green color vision in mammals. *Mol. Biol. Evol.* **15**, 560–567. (doi:10.1093/oxfordjournals.molbev.a025956)
  28. Komorowska J, Pisula W. 2003 Does changing levels of stress affect the characteristics of grooming behavior in rats? *Int. J. Comp. Psychol.* **16**, 237–246.
  29. de Waal FBM, Berger ML. 2000 Payment for labour in monkeys. *Nature* **404**, 563. (doi:10.1038/35007138)
  30. Dolivo V, Taborsky M. 2015 Cooperation among Norway rats: the importance of visual cues for reciprocal cooperation, and the role of coercion. *Ethology* **121**, 1071–1080. (doi:10.1111/eth.12421)
  31. Engqvist L. 2005 The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**, 967–971. (doi:10.1016/j.anbehav.2005.01.016)
  32. Zhang YH, Zhang JX. 2011 Urine-derived key volatiles may signal genetic relatedness in male rats. *Chem. Senses* **36**, 125–135. (doi:10.1093/chemse/bjq103)
  33. Schweinfurth MK, Taborsky M. 2016 No evidence for audience effects in reciprocal cooperation of Norway rats. *Ethology* **122**, 513–521. (doi:10.1111/eth.12499)
  34. Wenseleers T, Ratnieks FLW. 2006 Enforced altruism in insect societies. *Nature* **444**, 50. (doi:10.1038/444050a)
  35. Thompson FJ *et al.* 2017 Explaining negative kin discrimination in a cooperative mammal society. *Proc. Natl Acad. Sci. USA* **14**, 5207–5212. (doi:10.1073/pnas.1612235114)
  36. Stiver KA, Dierkes P, Taborsky M, Gibbs HL, Balshine S. 2005 Relatedness and helping in fish: examining the theoretical predictions. *Proc. R. Soc. B* **272**, 1593–1599. (doi:10.1098/rspb.2005.3123)
  37. Fischer S, Zöttl M, Groenewoud F, Taborsky B. 2014 Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. *Proc. R. Soc. B* **281**, 20140184. (doi:10.1098/rspb.2014.0184)
  38. Borgeaud C, Bshary R. 2015 Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Curr. Biol.* **25**, 3011–3016. (doi:10.1016/j.cub.2015.10.016)
  39. Calhoun JB. 1979 *The ecology and sociobiology of the Norway rat*. Bethesda, MD: U.S. Dept. of Health, Education, and Welfare, Public Health Service.
  40. Barnett SA. 1963 *The rat—a study in behavior* (AldineTransaction, A division of Transaction Publishers, Rutgers - The State University, New Jersey).
  41. Hamilton WD. 1964 The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)
  42. Marshall JAR, Rowe JE. 2003 Kin selection may inhibit the evolution of reciprocation. *J. Theor. Biol.* **222**, 331–335. (doi:10.1016/S0022-5193(03)00039-0)
  43. Queller DC. 1994 Genetic relatedness in viscous populations. *Evol. Ecol.* **8**, 70–73. (doi:10.1007/BF01237667)
  44. Griffin AS, West SA. 2002 Kin selection: fact and fiction. *Trends Ecol. Evol.* **17**, 15–21. (doi:10.1016/S0169-5347(01)02355-2)
  45. Calhoun JB. 1949 A method for self-control of population growth among mammals living in the wild. *Science* **109**, 333–335. (doi:10.1126/science.109.2831.333)
  46. Taylor PD. 1992 Altruism in viscous populations—an inclusive fitness model. *Evol. Ecol.* **6**, 352–356. (doi:10.1007/BF02270971)
  47. Stewart-Williams S. 2007 Altruism among kin vs. nonkin: effects of cost of help and reciprocal exchange. *Evol. Hum. Behav.* **28**, 193–198. (doi:10.1016/j.evolhumbehav.2007.01.002)
  48. Griffin AS, West SA. 2003 Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* **302**, 634–636. (doi:10.1126/science.1089402)
  49. Emlen ST, Wrege PH. 1988 The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.* **23**, 305–315. (doi:10.1007/BF00300577)
  50. Riehl C. 2013 Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B* **280**, 20132245. (doi:10.1098/rspb.2013.2245)
  51. Hamilton WD. 1963 The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356. (doi:10.1086/497114)
  52. Horner V, Carter DJ, Suchak M, de Waal FBM. 2011 Spontaneous prosocial choice by chimpanzees. *Proc. Natl Acad. Sci. USA* **108**, 13 847–13 851. (doi:10.1073/pnas.1111088108)
  53. Forbes D, Blom H, Kostmitsopoulos N, Moore G, Perretta G. 2007 *Euroguide on the accommodation and care of animals used for experimental and other scientific purposes*. London, UK: Federation of European Laboratory Animal Science Associations.
  54. Sharp J, Zammit T, Azar T, Lawson D. 2003 Stress-like responses to common procedures in individually and group-housed female rats. *J. Am. Assoc. Lab. Anim. Sci.* **42**, 9–18.